Biodiversity of the benthos off Kerguelen Islands: overview and perspectives

by

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ABSTRACT. - The Kerguelen Plateau possesses a very diverse benthic fauna. Over the years, the number of species recorded from the Kerguelen has substantially increased. From 172 species reported by Arnaud (1974), the total number of species has increased dramatically to 735 (Jouventin *et al*., 1996) and then to 960 in the present study. This area is particularly vulnerable to human activities and global climate change. Coastal benthic ecosystems are likely to be heavily impacted. However, these environments have been neglected and understudied during the last 30 years. The Kerguelen Plateau, situated at the northern limit of the Polar Front is probably one of the best study areas to (1) monitor the impact of climate forcing on coastal benthic assemblages; (2) assess the benthic community changes in relation to environmental forcing; and (3) assess the biodiversity of these benthic communities.

RÉSUMÉ. - Biodiversité du benthos des îles Kerguelen: vue d'ensemble et perspectives.

L'archipel des Kerguelen, y compris son plateau continental, se révèle, de par sa position géographique, posséder une biodiversité marine riche. L'exploration de cette biodiversité est loin d'être terminée comme le montrent les différents inventaires de la faune benthique. Le nombre d'espèces signalées dans cette zone augmente significativement comme en témoignent les inventaires successifs. Ce nombre, incluant seulement les invertébrés benthiques, passe de 172 (Arnaud, 1974) à 735 (Jouventin *et al.,* 1996), puis à 960 (présente étude). Cette région est soumise non seulement aux impacts anthropiques mais également aux impacts dus au changement climatique. Depuis ces 30 dernières années, les écosystèmes benthiques côtiers, lesquels sont directement affectés par ces perturbations, ont été négligés de toute étude globale. Dans un tel contexte, l'archipel des Kerguelen, situé à la limite nord du front polaire, se révèle une zone atelier idéale pour (1) analyser la réaction de ces écosystèmes aux perturbations de l'environnement, (2) déterminer l'évolution de ces communautés, et ce (3) sans oublier d'en explorer la biodiversité.

Key words. - Benthos - Biodiversity - Kerguelen Plateau - Climate change.

The Kerguelen Plateau is located just south of the Polar Front, and constitutes a natural obstacle to the eastward flow of the Antarctic Circumpolar Current (ACC) (Park *et al*., 2008). This area is especially favourable to primary production, and the benthic ecosystems are particularly diverse (Fig. 1).

What do we know about the benthic ecosystems around the Kerguelen Islands? More than 30 expeditions have surveyed the Kerguelen Plateau over the last 80 years (Hureau, 2011, this volume). However, few of them have collected benthic organisms. Between 1961 and 1970, numerous surveys were initiated by Arnaud, Délepine, Hureau and Rannou. Arnaud alone collected 76 dredges (2-218 m), five trawls (40-70 m), eight scuba dives and a large number of low tide, line, trammel, and hoop-net samples. Collecting was done mainly close to the coast, and in limited areas. However, they collected numerous specimens and led to a first estimate of the local biological diversity. The richest cruises for the quantity of benthos collected are MD03 and MD04 (1974 and 1975 respectively) on the research vessel "*Marion Dufresne*". The purpose of these cruises was to obtain quantitative and qualitative data on benthos and demersal fishes. During the MD04 survey, 122 stations (234 samples) were made in 10 radial transects around the Kerguelen Islands, with depths ranging from 17 to 4340 m (Fig. 2). The specimens dredged during these cruises are now housed in the Muséum national d'Histoire naturelle (MNHN, Paris), mostly fixed in formalin and later preserved in ethanol. The majority of the specimens have already been studied, although a number of them are still to be sorted and studied. More recently, the POKER II survey (August-October 2010) collected a large number of specimens on the Kerguelen continental shelf (Fig. 3), with 200 collecting events at depths ranging from 100 to 1000 m. Remaining samples

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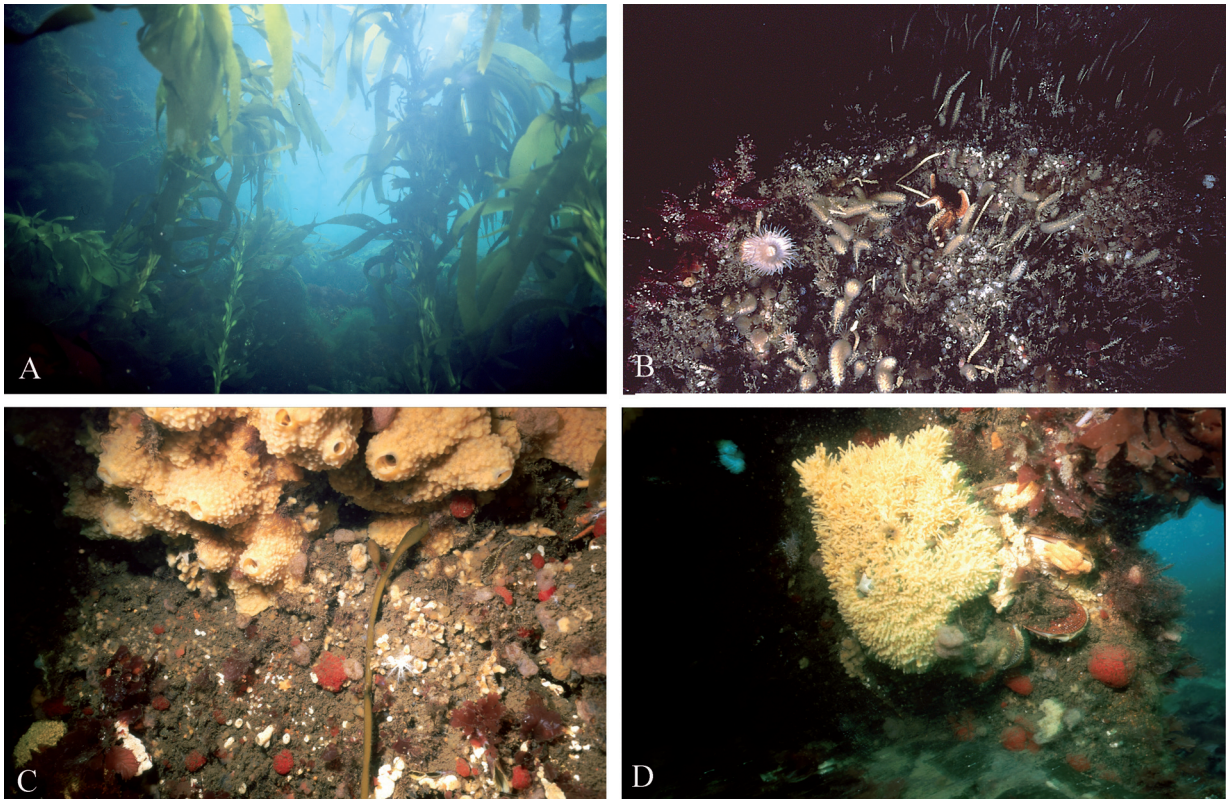

Figure 1. - Benthic diversity of the Kerguelen coastal ecosystems. **A**: *Macrocystis* dominated benthic assemblage, île aux Moules; **B**: Hard substrate benthic assemblage dominated by hydozoans, Port-Christmas; **C** and **D**: Hard substrate benthic assemblage dominated by sponges, Port-aux-Français. Credit: © photos programme IFRTP n°195 - benthos-mac, courtesy of J.P. Féral.

were frozen for future analysis. The specimens will be distributed to experts of the various groups. They are currently being sorted by morphospecies, catalogued in the collection database, and transferred to ethanol for longer term storage. For every collecting event, at least one sample from each morphospecies is taken for DNA barcoding.

The macrofauna from the benthic ecosystems from the Kerguelen Plateau includes a large number of suspension feeders. Some taxa are very diverse or represented by a large number of specimens, like sponges, polychaetes, cnidarians, bryozoans, pycnogonids, crustaceans, echinoderms and ascidians. Many species are eurybathic. For example, the sea anemone *Stomphia selaginella* (Stephenson, 1918) ranges from 9 to 1700 m, the sponge *Stylocordyla borealis* (Loven, 1868) ranges from 13 to 2880 m, and the pycnogonid *Colossendeis megalonyx* (Fry & Hedgpeth, 1969) ranges from 7 to 4900 m. Brooding is very common across all phyla. In the benthos, 50 to 70% of species are brooders; however, reproductive strategies vary widely. Evaluating the proportion of endemism is difficult, as is eurybathy. Some species currently considered to be endemic might only appear so because of our largely incomplete knowledge of the Southern Ocean biodiversity. However, all phyla appear to include at least a few species only known from the Kerguelen Islands.

An abundant literature about the impact of the global climate change in the Southern Ocean covers the marine ecosystems and biota, including the top predators (seabirds and marine mammals, among others see Barbraud *et al.,* 2000; Croxall *et al*., 2002; Georges and Le Maho, 2003; Peck *et al*., 2004; Pörtner, 2006; Aronson *et al.,* 2007; Barnes and Peck, 2008; Whitehouse *et al*., 2008 ; Clarke *et al.,* 2009; Gutt *et al*., 2010). This impact has been relatively well studied for the terrestrial fauna (Chapuis *et al*., 1994; Chevrier *et al*., 1997; Frénot *et al*., 2006) and flora (Frénot *et al*., 2001, 2005, 2006) of the Kerguelen Islands. For the marine fauna, only mammals (Weimerskirch *et al*., 2003 ; Bailleul *et al*., 2007) and birds (Gauthier *et al*., 2002; Lescroël and Bost, 2006; Lescroël *et al*., 2009) have been studied.

The benthos, which represents the major component of the marine biodiversity, has not been investigated in such detail. Still, there is no doubt that at least some alterations of the environment, and therefore the benthic ecosystems have happened in the last decades. The acceleration of erosion on the islands is the result of the combined effects of the desertification resulting from global changes (lower rainfalls

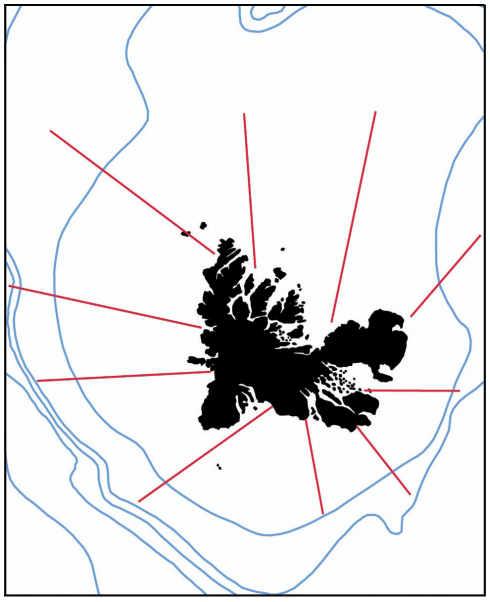

Figure 2. - MD04 - Benthos survey (February-March 1975) radials of stations on the Kerguelen Plateau, modified from Guille (1977).

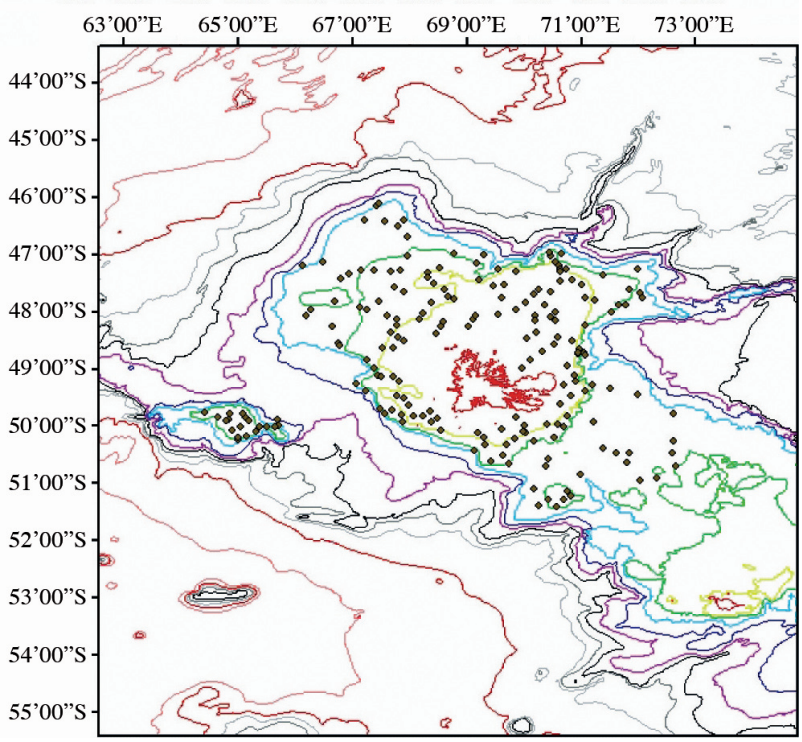

Figure 3. - POKER II survey (August-October 2010) station locations on the Kerguelen Plateau, courtesy of G. Duhamel.

and higher temperature) and of the grazing by the introduced European rabbit (*Oryctolagus cuniculus*) (Whiman *et al.*, 2006). Most of these detrital particles are washed into the ocean, and probably alter the benthic ecosystems dominated by filter feeders. Modifications are expected at diverse levels, be it populational, behavioural or maybe even in the phenotypic expression and therefore, morphology. Human activities might also have caused the introduction of alien species through ship hull fouling or discharge of ballast water.

In such a context, many questions arise. Did the benthic communities change in the last 30 years? How do the benthic coastal ecosystems around the Kerguelen Islands react to environmental changes? Before we can provide answers to these questions, we need a synthesis of the current state of the Kerguelen biodiversity. This synthesis should compare the fauna *in situ* to all the existing data, either through literature or yet unstudied collection of preserved specimens. In this paper, we present an overview of the benthic diversity of the Kerguelen Plateau. We also list the main lines of research necessary to understand the evolution of the Kerguelen marine ecosystems.

RESULTS

Research on the collected benthos was for the largest part, performed immediately after the cruises, between 1965 and 1980 (first period). It was resumed between 1990 and 2010 (second period). However, no recent synthesis is available on the macrobenthic diversity, contrary to Antarctic regions like the Ross Sea (Rehm *et al.*, 2006), the South Shetland Islands (Piepenburg *et al.*, 2002), or the Weddell Sea (Jones *et al.*, 2007; Linse *et al.*, 2007). We will concentrate here on benthic invertebrates, not taking into consideration the flora or the demersal fishes.

During the first period, distribution and biomass data were published on the species with commercial interest: lithodids, crabs, cephalopods, gastropods, bivalves, etc. (Arnaud 1987a, 1987b, 1987c; Roper *et al.*, 1987). For non-commercial species, only inventories are available, and they are based on morphological identification (for references, see each taxa). Arnaud published the first synthesis on the Kerguelen benthos in 1974, and identified 172 species (Tab. I), Jouventin *et al.* (1996) recognized 735 benthic species, and the present study lists 960 benthic species.

Cnidaria

Arnaud (1974) lists five species of Hydrozoa. Watson (2008) added one species to this. Two species of Anthozoa collected during MD03 were listed by Millard (1977). Another was collected during the Soviet surveys on the Kerguelen continental shelf (Stepanjants, 1979), and one more by Peña Cantero and Vervoort (2003). A single Stauromedusae species is known from the area (Vanhöven, 1908; Miranda *et al.*, 2009).

Table I. - The best available estimates of higher taxon species richness for benthic marine invertebrates on the Kerguelen Plateau as of January 2011. The tabulated data are from Arnaud (1974), Jouventin *et al*. (1996) and this study.

Phylum/ Subphylum	Class	Arnaud, 1974	Jouventin *et al*., 1996	This study
Porifera	Desmopongiae	3	87	95
	Calcarea	-	12	13
	Hexactinellida	-	-	3
Cnidaria	Hydrozoa	5	-	6
	Anthozoa	-	-	4
	Staurozoa	-	-	1
Nemertinea		-	-	1
Brachiopoda		-	4	7
Bryozoa		-	-	58
Polychaeta		29	108	109
Mollusca	Gastropoda	24	107	131
	Bivalvia	15	29	30
	Solenogastre	-	4	4
	Polyplacophora	2	3	6
	Scaphopoda	-	1	1
	Cephalopoda	-	8	25
Crustacea	Malacostraca (Amphipoda)	42	84	85
	Malacostraca (Isopoda)	15	54	54
	Malacostraca (Tanaidacea)	1	20	20
	Malacostraca (Mysidacea)	-	20	20
	Malacostraca (Cumacea)	-	20	20
	Malacostraca (Decapoda)	4	6	20
Chelicerata	Pycnogonida	10	21	51
Echinodermata	Echinoidea	2	6	10
	Holothuroidea	2	29	34
	Ophiuroidea	2	15	18
	Asteroidea	6	29	35
	Crinoidea	1	1	6
Tunicata	Ascidiacea	9	67	93
Total		**172**	**735**	**960**

Porifera

Arnaud (1974) reports the presence of three Demospongiae species whereas this study lists 95 species (Tab. I). Boury-Esnault and Van Beveren (1982) reported 77 species of Demospongiae including 14 new species (Tab. II). Sara *et al*. (1992) listed 95 species of Desmospongiae, many of which have circumpolar distribution. Estimates of species richness for the Demospongiae in the Southern Ocean vary from 300 to 352 (Sara *et al*., 1992; Arntz *et al*., 1997), and 27% to 32% are present on the Kerguelen Plateau. Borojevic and Grua (1965) reported 13 species of Calcarea, and Janussen *et al*. (2004) listed three species of Hexactinellida. Sponges locally dominate the benthic biomass. Sponge-dominated assemblages constitute potential habitats for colonizing epibionts and are essential in structuring of the benthic community.

Bryozoa

Fifty-eight species of bryozoans have been recorded from studies of d'Hondt and Redier (1977) and d'Hondt (1984). Five of them have been described since 1977 (Tab. II). The species diversity of this group in the area might be underestimated. Kuklinski and Barnes are currently reassessing the knowledge of the group for the Kerguelen Plateau using the fauna collected during the POKER II cruise. Their work aims at integrating bryozoan diversity at a broader Southern Ocean scale.

Tunicata

The total number of ascidian species increased dramatically from 9 recognised by Arnaud (1974) to 67 (Jouventin *et al*., 1996) and to 93 (this review, Tab. I). Twenty eight of these species have been described since 1970 (Monniot, 1970; Monniot and Monniot, 1974; Monniot and Monniot, 1977; Monniot, 1978a, 1978b; Monniot and Gaill, 1978; Millar 1982; Tab. II). Of the 237 species that have been recorded from the Antarctic, Subantarctic and South American areas, 39% are represented on the Kerguelen Plateau. This area is probably the region where ascidians represent the most important proportion of the total biomass. This fauna is diversified with a number of species similar to that of the European or North-American waters (Monniot and Monniot, 1983; Primo and Vazquez, 2007). Salps and Appendicularia are not surveyed in this review.

Table II. - Number of benthic marine invertebrate species described between 1970 and 2010 from the Kerguelen Plateau.

Phylum	New species	Authors	Date
Porifera	14	Boury-Esnault & Van Beveren	1982
Brachiopoda	1	Cooper	1981
Bryozoa	5	d'Hondt & Redier	1977
Mollusca	1	Vicente	1974
	1	Adam	1974
	4	Salvini-Plawen	1978
	3	Ponder	1983
	1	Osorio & Arnaud	1984
	2	Waren, Arnaud & Cantera	1986
	1	Houart	1997
Echinodermata	1	David & Mooi	2000
	2	Guille	1982
	1	O'Loughlin	2009
	1	Eléaume *et al.*	in press
Crustacea	1	Shiino	1970
	9	Bellan-Santini & Ledoyer	1974
	1	Kensley	1975
	5	Kensley	1980
	6	Ledoyer	1977
	3	Carvacho	1977
	8	Shiino	1978
	1	Broyer De	1985
	1	Macpherson	1988
Chelicerata	1	Pushkin	1975
	1	Pushkin	1976
	1	Pushkin	1977
	1	Pushkin	1984
	2	Pushkin	1993
	2	Child	1994
	1	Child	1995
Tunicate	3	Monniot	1970
	2	Monniot & Monniot	1974
	4	Monniot & Monniot	1977
	11	Monniot	1978 a-b
	7	Monniot & Gaill	1978
	1	Monniot & Monniot	1983

Echinodermata

Echinoderms as a whole are likely to represent an important part of the total biomass, although their proportion has not been precisely evaluated. Not all the five classes have been studied to the same degree of precision. Sea stars from the Kerguelen Plateau have not been reviewed for decades, whereas ophiuroids were given some attention by Guille (1982) and recent syntheses for echinoids and holothurians are available (see David *et al.*, 2005; O'Loughlin, 2009). Table I shows the increase in the number of echinoderm species from 10, 80 to 105 (Arnaud, 1974, Jouventin *et al.*, 1996, and this review, respectively). Table II lists six new species identified. Among the echinoderms, the number of crinoid species increased the most proportionally. A single species, *Promachocrinus kerguelensis*, was recognized by Arnaud (1974) and Jouventin *et al.* (1996). The preliminary results of the current study show the presence of six species on the Kerguelen Plateau. A new stalked crinoid attributed to the genus *Ptilocrinus* (Eléaume *et al.*, in press) was caught by long lines during recent fishing cruises. Several additional specimens have been dredged during the 2010 POKER II cruise. This is the first record of stalked crinoids from the Kerguelen Plateau.

Crustacea

The number of crustacean species increased from 62 (Arnaud, 1974), to 204 (Jouventin *et al.*, 1996) and then to 219 (this review, Tab. I), with descriptions of 35 new species since 1970 (Tab. II). However, most of the studies date back to the 1970's (Bellan-Santini and Ledoyer, 1974; Carvacho, 1977; Ledoyer 1974, 1977; Shiino, 1978). For this study, only decapods were investigated. Gorny (1999) reported 17 species from the Kerguelen Plateau. Macpherson (2004) improved the checklist and included three more species. The total number of decapod species is now at 20, which contrasts with the four species identified by Arnaud (1974) and the six species of Jouventin *et al.* (1996) (Tab. I).

Pycnogonida

Munilla and Soler Membrives (2009) recently published a checklist and revision of the pycnogonids. The authors reported 33 species (compared to 10 by Arnaud (1972), see Tab. I), including nine new species (Tab. II). Most are deep species. A total of 264 species have been recorded in the Antarctic, Subantarctic and South American areas, and 12.5 % of this diversity is represented around the Kerguelen Islands.

Annelida

This review (Tab. I) records the latest inventory of polychaetes at 109 (29 species by Arnaud, 1974 and 108 species by Jouventin *et al.*, 1996). Since the publications of Rullier (1973), Bellan (1975), Desbruyères (1976) and Duchêne (1984), no new inventory was made on this phylum for the area. The polychaete fauna represents an important biomass and can constitute from 20 to 75% of the total macrofauna, especially in the infralittoral and the circalittoral muddy environments (Duchêne, 1984).

Mollusca

Table I shows the increase in the number of molluscan species from 41, 152 to 197 (Arnaud, 1974, Jouventin *et al.*, 1996, and this review, respectively). Table II lists 13 new species identified. Arnaud (1984) and Canteras and Arnaud (1985) published the last noteworthy gastropod inventories. Troncoso *et al.* (2001) reviewed the gastropods and the bivalves, later improved by Aldea and Troncoso (2010). Cherel *et al.* (2004) have considerably increased the number

of known cephalopods (both benthic and pelagic) from the Kerguelen Plateau.

Brachiopoda

Four species of brachiopods were recorded by d'Hondt (1977) Three species were added by Cooper (1981, Tab. I), including the description of a new species (Tab. II). Gaspard is currently reassessing the diversity of the group in the broader context of the whole Southern Ocean.

Nemertinea

Riser (1974) reports the presence of a single species of Nemertinea (Tab. I).

DISCUSSION

Jouventin *et al*. (1996) did not include in their review cnidarians and bryozoans, two major components of the Kerguelen ecosystems. Our review adds to these older studies, but is far from being exhaustive. However, each new synthesis displays an increase in the number of species, from n=172 in Arnaud (1974) to n=960 in this review (Tab. I). Reasons for this are diverse. The exploration of Arnaud was restricted to the biodiversity of the coastal region of some localities of the Kerguelen Islands. The surveys MD03 (1974) and MD04 (1975) (Fig. 2) investigated larger areas on the Kerguelen Plateau, at depths ranging from 17 m to 4340 m. The diversity in this area is higher than where Arnaud collected, explaining the higher number of species in the review by Jouventin *et al*. (1996). The present review incorporates the data published by Arnaud (1974) and Jouventin *et al*. (1996), as well as the results from the Russian surveys and the recent publications. However, most of the species added in the present study come from the MD03 and MD04 surveys. The specimens collected during large surveys are generally studied a long time after the cruise took place (e.g., David and Mooi, 2000; Eléaume, 2004; Macpherson, 2004). In some zoological groups, specimens from MD03 and MD04 are still being studied (e.g., crinoids, brachiopods). Delays in collection-based studies are best explained by excessive workloads for the few competent taxonomists, neglect by taxonomists of a given geographical area (either by lack of interest or because another region is prioritized) or the lack of a trained taxonomist. Another reason for the increasing number of species listed depends on the degree of precision of the reviews. Jouventin *et al*. (1996) mostly concentrated on the major publications of description of the fauna (e.g., Boury-Esnault and Van Beveren, 1982; Monniot and Monniot, 1983; Duchêne 1984). The present review tried to be comprehensive, however the effort to collect the relevant literature must be continued.

Many studies tend to show a close affinity between high Antarctic and Subantarctic fauna. Monniot and Monniot (1983) describe the Antarctic and Subantarctic ascidians as a homogeneous assembly, geographically isolated. A recent, more complete analysis including material from the Bellingshausen Sea confirms these results (Primo and Vazquez, 2009). Faunal affinities between the Antarctic and Kerguelen shelves are also found in sponges (Sara *et al*., 1992; Tabachnik, 1994), cheilostome bryozoans (Barnes and De Grave, 2000; Barnes and Griffiths, 2008), polychaetes (Desbruyères, 1976; Sicinski and Gillet, 2002), bivalves and shelled gastropods (Arnaud, 1984; Linse *et al*., 2006). However, the high rate of cryptic speciation found on the Antarctic continental shelf suggests that further molecular studies are likely to unveil hidden diversity, and morphologically similar species may prove to be genetically distinct.

PERSPECTIVE

In order to better understand the diversity, distribution, connectivity, ecological niche and evolutionary processes and patterns of the Kerguelen benthic fauna we propose three main lines of research.

1. Further explore the Kerguelen biodiversity

The exploration of the diversity of the benthic fauna in the area is far from complete. Major groups like bryozoans, sponges and cnidarians have not been studied recently, and only a part of the available specimens has been analyzed. The diversity of cnidarians is probably largely underestimated, although they dominate in assemblages locally. The small number of studies explains this lack of data, which will be at least partially filled by the molecular barcoding (Hajibabaei *et al*., 2007) of the specimens from the POKER II survey. Barcoding has already been started on some groups, mostly vertebrates (Duhamel *et al*., 2010; Smith *et al*., 2011), and will be used much more broadly for identification and preliminary taxonomic overview as was done elsewhere (Dettai *et al*., in press; Rock *et al*., 2008). Some groups have been seldom studied, like echiurans, nemerteans, hemichordates, sipunculid worms. Sampling techniques used were not adapted to collecting small sized benthic species, and therefore, it is likely that much remains to be discovered for these particular groups.

2. Understand the evolution of the diversity

Once a reliable checklist of biota is available, the speciation processes and patterns can be studied. Testing for the presence of species flocks would allow to determine the patterns of adaptative radiations that may have occurred on this large Subantarctic peri-insular shelf, as has been proposed (and is being tested) for the Southern Ocean (Lecointre *et*

al., 2011). Molecular studies on several groups have shown that the fauna of the Kerguelen Plateau is essential to our understanding of the evolutionary patterns in the Southern Ocean (Duhamel *et al*., 2010).

3. Predict climate change impact

This requires the establishment of a new baseline using modern techniques, to compare past and present collections. This baseline would include lists of benthic organisms, characterisation of the benthic communities, knowledge of the key species for the ecosystems (biomass, distribution, function) and the interrelationship between biotic (physiology and behaviour of key species) and abiotic factors such as substrate type, bottom current velocity and direction (Eléaume *et al*. 2010), bottom temperature, bottom conductivity, seabed topography. The MD03 and MD04 surveys constitute a unique past collection from 35 years ago. It includes specimens housed at the MNHN, as well as complementary data such as substrate type, and can serve as a temporal reference for comparison with new surveys. The MNHN also has developed a strong expertise through studying similar issues in the Dumont d'Urville Sea on many groups. The comparison between the different samples and data will allow us to establish distribution maps of the organisms according to the main abiotic features, leading to an eco-bioregionalisation map of the Kerguelen Plateau. Climate change consequences could also be monitored.

In order to fulfill these three lines of research we first need to identify the available data. Then, we need to identify the specimens and study the evolution of the groups through two main approaches: morphology and molecular systematics. The samples collected on the POKER II survey are being studied, but the sampling must also be completed with additional field surveys. The MD04 radial transects as well as additional stations closer to the shore and further at sea (Fig. 2) must be sampled, or at the very least a few strategically selected transects. The sampling must be performed using modern investigating techniques, including characterisation of substrate type (grab, box corer), current flow measurements (ADCP), conductivity, temperature and depth (CTD), bottom topography (multibeam sonar) and underwater videos. Videos provide unique data about the behaviour of the organisms and the benthic assemblages and coverage of megazoobenthos (Gutt *et al*., 2007). Modern sampling techniques and modern study techniques like molecular systematics need to be generalized, as they are the key to further discoveries. In parallel, observations in an aquarium setting are needed for the investigation of the behaviour and physiology of key species.

The development of molecular techniques and of new sampling techniques will give a much needed boost to the study of the benthic faunas. They will help to characterize the optimal habitats of many taxa. In addition to a biodiversity exploration, the deliverables will include guides to species identification, Computer Aided Identification (CAI), and molecular identification. The extension of the exploration of the Kerguelen Plateau will contribute to the management of the Marine Nature Reserve by adding complementary reference data points on biodiversity and assemblages. The mapping of the substrate types will be helpful for the management and conservation of the biodiversity in the Kerguelen Marine Nature Reserve.

Acknowledgements. - We are thankful to Guy Duhamel for advice. We also wish to thank Pierre Lozouet for helping track the literature used in this review, as well as for his insightful remarks on mollusks. We are also indebted to D. Welsford who reviewed this paper.

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